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Report

Flexibility of Timing of Avian Migration to Climate Change Masked by Environmental Constraints En Route

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Summary

During the past decades, phenology of many organisms has advanced in response to climate change [1]. Earlier arrival of long-distance migrants has been reported frequently [2, 3], but advancements of arrival and breeding were not always sufficient to match phenology at other trophic levels [4]. This has led to increased selection for early breeding [5] and severe population declines [6, 7]. This inadequate response has been explained by an inflexible start of migration, governed by cues unrelated to climate change, such as photoperiod [8]. It has been suggested that evolution at the genetic level is required for a change in photoresponsiveness [9]. Recently, such an evolutionary change in migration timing was suggested [10]. Here I show that timing of spring migration of pied flycatchers (*Ficedula hypoleuca*) has responded flexibly to climate change. Recovery dates during spring migration in Northern Africa advanced by ten days between 1980 and 2002, which was explained by improving Sahel rainfall and a phenotypic effect of birth date. The lack of advance on the breeding grounds most likely was due to environmental constraints during migration. Adjustment of arrival date in migrants to climate change could thus be rapid, but only if circumstances favorably change for the whole journey.

Results and Discussion

The subject of this analysis, the pied flycatcher (*Ficedula hypoleuca*), is one of the most widely studied species in terms of examining the effect of climate change on breeding dates. Previous work has shown that trends in breeding dates were affected by local temperature changes across Europe [11] and that these responses were less than the peak date of food for chicks warranted [5], a consequence of unchanged arrival dates [12], which led to population declines [6]. Pied flycatchers winter in sub-Saharan Western Africa and breed in Europe and Western Asia [13]. For my analyses, I used all (n = 245) recoveries of pied flycatchers ringed as nestlings in their European breeding areas (more than 2.2 million nestlings ringed in total) and recovered during spring migration in Northern Africa (Figure 1A). The median recovery date during spring migration was strongly correlated with latitude and longitude of birth, being later for birds originating from more northern and eastern populations (Figure 1B). A similar effect of latitude was found on laying dates [14] and arrival dates (Figure 1B). On the basis of population-specific median African spring recovery and breeding site arrival dates, spring migration speed approximated 360 km/day, 300 km/day, and 270 km/day for birds breeding at 52°N, 60°N, and 65°N, respectively. These speeds may be overestimated, because birds could be dead for several days before being found, but are similar to individual tracks of passerines measured with geolocators [15]. Central and Western European populations have especially limited opportunity to speed up their migration during the European part of the journey, because they travel at high speeds in just six days, whereas the food peak in their environment has advanced by 15 days in the last two decades [16].

Migration dates through Northern Africa have changed since 1950, with an initial delay until 1980 and a clear advancement of about 10 days since then (Table 1; Figure 2A). This advance contrasts with the unchanged arrival dates of the first arriving males on the Western and Central European breeding grounds [12]. This supposed inflexibility in migration dates has been hypothesized to result in a mismatch of breeding time with other trophic levels [5]. The observed change in spring migration date in Northern Africa held up after statistically accounting for birth origin, age, and recovery location and hence cannot be a consequence of a change in population composition of recovered birds, varying in migration date. A similar advance in migration dates since 1980 has been shown for pied flycatchers and other long-distance migrants by Jonzén et al. in Italy [10]. These authors suggested that the advanced migration date was likely due to an evolutionary response caused by climate change. This would be an important claim, because if evolutionary changes occur so quickly, the observed insufficient adjustment of timing of arrival to climate change [5, 6, 17] is likely to be an only temporary problem, quickly solved by evolution.

In the data considered here, the trend in spring migration date over the years could be explained by a phenotypic effect of individual birth date (Table 1; Figure 3) and annual fluctuations in Sahel rainfall in the preceding winter (Figure 2B). The effect of Sahel rainfall was that in years with more rainfall, birds were recovered at earlier dates, and the apparent delay in migration dates from 1950 to 1980 is likely to be caused by the increasing droughts, whereas the recent advance in migration dates was during a period with increasing rainfall [18]. The effect of birth date is more complicated, because the effect interacts with birth latitude (Figure 3): at more southern breeding grounds, later birth dates were associated with later recovery dates in Northern Africa, whereas for more northern breeding grounds, later birth dates were associated with earlier recovery dates. Part of the change in recovery dates over the years could hence be explained by the advanced breeding dates since 1980, which were most pronounced in Western and Central Europe [11]. It is unlikely that the effect of birth date is a genetic effect; otherwise, early-born birds would be expected to also breed early themselves and hence have early-born chicks. This was not found in a Dutch breeding population: the laying date, relative to the annual mean, of locally born females in their first breeding year was unrelated to birth date (the slope was 0.07 [standard error (SE): 0.06] days advance for each day of earlier birth, $F_{1,344} = 1.32$,

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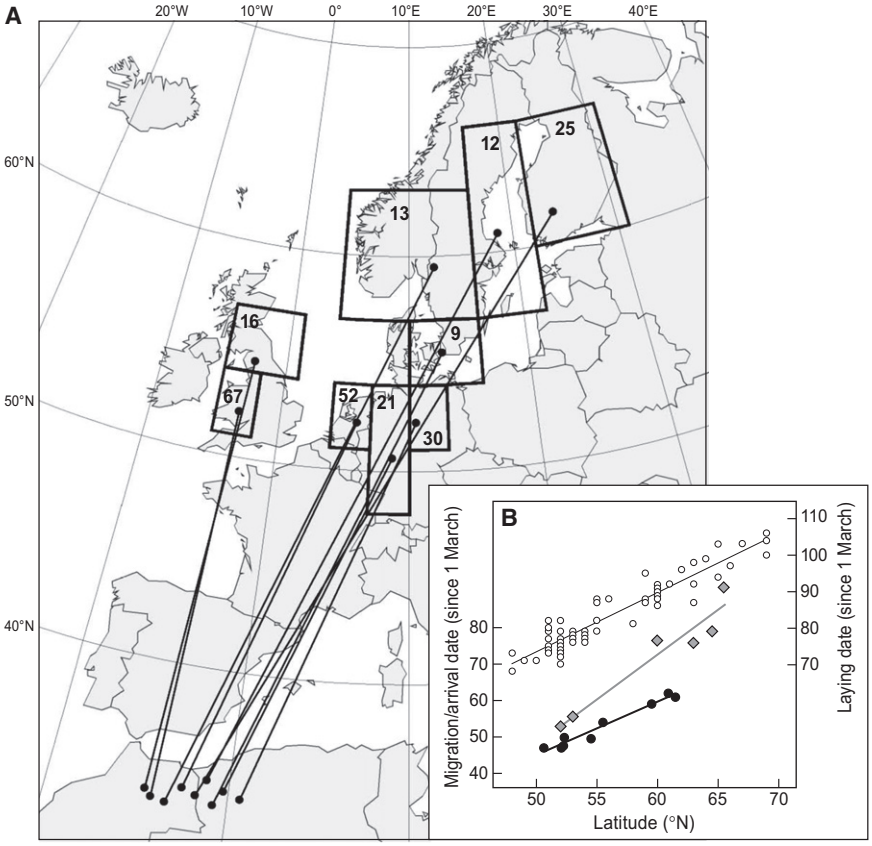

Figure 1. Timing and Position of Spring Recovery Dates in Relation to Birth Dates of Pied Flycatchers Ringed across Their European Breeding Area

(A) Map of mean locations of ringing and recovery site of pied flycatchers ringed as nestlings, grouped on the basis of breeding site. Numbers indicate sample sizes.

(B) Median spring recovery dates in Northern Africa (●), mean laying dates (○), and mean arrival dates (◇) of pied flycatcher populations in relation to breeding latitude. For the recovery data, I averaged all data from birds born in blocks of at least 3° latitude × 3° longitude. Data on laying dates were taken from Sanz [14]. A general linear modeling analysis of spring recovery date in Northern Africa showed that it was related to both natal latitude and longitude (recovery date = −16.14 + 1.22 [0.12] × latitude + 0.15 [0.06] × longitude; latitude: $F_{1,6}$ = 99.60 $p < 0.001$, longitude: $F_{1,6}$ = 7.18 $p < 0.037$; estimates of significant parameters [and their standard errors] are given). Spring arrival date at the breeding grounds was related to latitude of the breeding site (arrival date = −64.14 + 2.28 [0.31] × latitude; $F_{1,4}$ = 55.64 p = 0.002). Population mean laying date of different populations was related to latitude, longitude, and altitude of the site (laying date = 0.02 + 1.42 [0.082] × latitude + 0.15 [0.055] longitude + 0.0085 [0.0021] × altitude; latitude: $F_{1,63}$ = 301.02, $p < 0.001$; longitude: $F_{1,63}$ = 16.40, $p < 0.001$; altitude: $F_{1,63}$ = 2.74, $p < 0.008$).

p = 0.25) and was 3.40 (SE: 0.80) days later for females in their first year of life ($F_{1,344}$ = 18.23, $p < 0.001$). In this population, we have not found a significant heritability of laying date [5]. A genetic cause also would not explain the interaction between birth date and latitude. As a possible mechanism for the interaction between birth latitude and birth date, I propose an effect of photoperiod during early life: southern-born nestlings experience longer days the later they are born, whereas the reverse is true for northern-born young (see Figure 3). Such an effect of photoperiod has been experimentally shown for blackcap (*Sylvia atricapilla*) nestlings exposed to a photoperiod mimicking an earlier time of year, which subsequently advance their timing of autumn molt and migration [19]. I therefore propose that a mere advance in hatching dates in response to climate change as observed in many bird species could result in an advance in migration dates as well. This ontogenetic effect helps the birds to quickly respond to directional changes in climate.

Directional changes in migration date in response to climate change could be due to phenotypic and/or genetic responses. Correlations between environmental parameters en route and arrival date demonstrate phenotypic responses. These responses are bound to be limited if departure dates are inflexible, and previously it has been suggested that a genetic response is needed for a change in departure date [20]. Phenotypic responses in departure date to environmental conditions at the wintering sites have been observed [21, 22], but these have limited value if winter conditions have low predictive value for the onset of spring. The observed effect of birth date on migration date presented here suggests phenotypic plasticity in departure date, allowing birds to change migration time in response to advanced breeding dates.

The advanced migration dates observed in this study are in stark contrast with the lack of changes in arrival dates at the breeding grounds [12] and contradict the popular hypothesis that long-distance migrants adapt insufficiently to climate change because their spring departure schedules cannot

Table 1. Variables Explaining Variation in Individual Spring Recovery Dates of Pied Flycatchers in Northern Africa

	Coefficient	Standard Error	Wald	p
Recovery year	−0.12	0.11	9.5	0.002
Recovery year^2	−0.019	0.007		
Birth latitude	0.135	0.42	0.986	
Birth longitude	0.095	0.167	0.325	0.576
Recovery latitude	1.093	0.504	4.93	0.026
Recovery age	−111.226	26.67	6.45	
Age × birth latitude	1.977	0.494	15.7	<0.001
Sahel rainfall	−2.638	1.17	5.151	0.023
Birth latitude	8.32	3.583	0.013	
Birth longitude	0.339	0.147	5.319	0.021
Recovery latitude	1.14	0.493	5.375	0.024
Ringing date	4.524	1.685	2.236	
Recovery age	−110.593	26.324	5.899	
Birth latitude × ringing date	−0.079	0.032	6.398	0.011
Age × birth latitude	1.971	0.488	16.39	<0.001

The top seven data rows show effects of year, birth, recovery locality, and recovery age. The bottom eight data rows show effects of ecologically important factors that could replace the effect of year: Sahel rainfall and individual variation in birth date. Results are from a mixed-effects model, with year as a random effect. p values are not given for main effects if they were in significant interactions. In the first model, the effect of recovery year and its quadratic effect were tested simultaneously with two degrees of freedom. In the second model, year and its squared term were no longer significant (Wald statistic = 3.686, df = 2, p = 0.158).

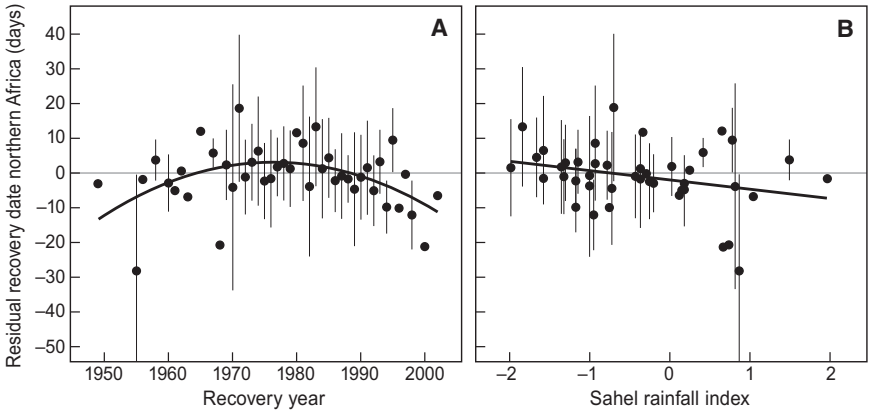

Figure 2. Spring Recovery Dates of Pied Flycatchers in Northern Africa in Relation to Recovery Year and Sahel Rainfall

(A) Change over time for mean (± standard deviation [SD]) spring recovery date of pied flycatchers in Northern Africa during the period 1949–2003. Residual recovery dates are presented from a model including birth and recovery latitude, bird age, and the interaction of age × birth latitude (see Table 1A for analysis).

(B) The effect of annual Sahel rainfall index on mean (± SD) spring recovery date of pied flycatchers in Northern Africa during the period 1949–2003. Residual recovery dates are presented from a model including birth and recovery latitude, birth longitude, bird age, nestling ringing date, and the interactions of age × birth latitude and age × nestling ringing date (see Table 1B for analysis).

anticipate the changes in phenology at the breeding grounds [5]. As alternative to this inflexibility hypothesis, I propose that migration timing could react flexibly to past conditions at the breeding grounds, but that this flexibility is masked because of environmental constraints encountered during migration. One major constraint could be weather conditions during migration, especially for obligate insectivores such as the pied flycatcher. Temperature has been shown to be an important factor in determining migration speed [23, 24], and indeed, the temperatures that pied flycatchers encounter during migration from Northern Africa to breeding sites at 52°N have not increased between 1980 and 2001 (Figures 4A and 4B). If the observed advancement of migration date through Northern Africa were followed by continuation of migration to the Central European breeding grounds, this would mean that the birds migrate and arrive at lower temperatures. The costs of migrating earlier in the spring, when temperatures are lower, are higher energy expenditure [25], lower food availability (aerial insect abundance), and shorter days, probably resulting in lower survival [26]. If these constraints are released, birds could advance their spring arrival, as has been shown for Finnish pied flycatchers, which migrate at later dates through Europe. Because temperatures have increased at their migration time, this population has advanced spring arrival in recent decades [23, 27]. Environmental constraints during migration thus could mask the ongoing earlier onset of migration, despite strong selection to breed earlier in the year.

The observed phenotypic plasticity could allow a rapid response to climate change if circumstances all along the migratory route change favorably. At present, this is not happening, and it is unknown whether the steeper increase in temperature during particular periods in spring is a fundamental feature of the current climate change or not. The geographic variation in temporal structure of temperature change now acts as a major problem: in many sites in Central and Western Europe, temperatures in the period before migration have not increased (Figures 4A and 4B), in contrast to the period after migration, which has shown strong increases in temperature (Figure 4C). Thus, long-distance migrants are caught between unfavorable conditions during their migratory period and a strong temperature increase after they reach their breeding grounds, resulting in a stronger advance in the peak in food availability compared to the birds' arrival and breeding date. In present environmental conditions, birds could only maintain (or restore) the match with the food peak if they migrate earlier and simultaneously get better at surviving colder conditions during migration and arrival, and/or switch to an alternative diet. The constraints along the European part of the migratory route may be released by ongoing climate change, but projections for Sahel rainfall are negative [28], posing an extra constraint on the birds' life-cycle adaptation to the advanced phenology of their breeding grounds in the coming decades. This also implies that little should be expected in terms of an evolutionary response: any genetic variation in spring departure is likely to be masked by environmental constraints and not translated into earlier arrival. More generally, because climate change often alters temperatures differently at different periods in the year, adaptation of life cycles in animals with a complex annual cycle is not likely to

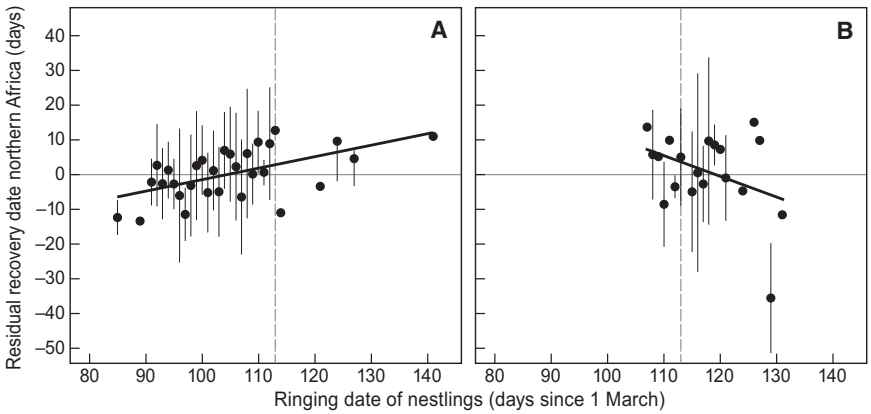

Figure 3. Relationship between Northern African Recovery Date during Spring Migration and Nestling Ringing Date of Pied Flycatchers from Different Latitudes

For graphical purposes, data were divided into two ringing latitude categories, birds born south of 57°N (A) and birds born north of 57°N (B), to show the different effects of latitude on the correlation between ringing date and recovery date. The dashed vertical line indicates the date of the solstice. Also for graphical purposes, data are plotted as means ± SD per day, but statistics are performed on individual data points. Statistics are given in Table 1B.

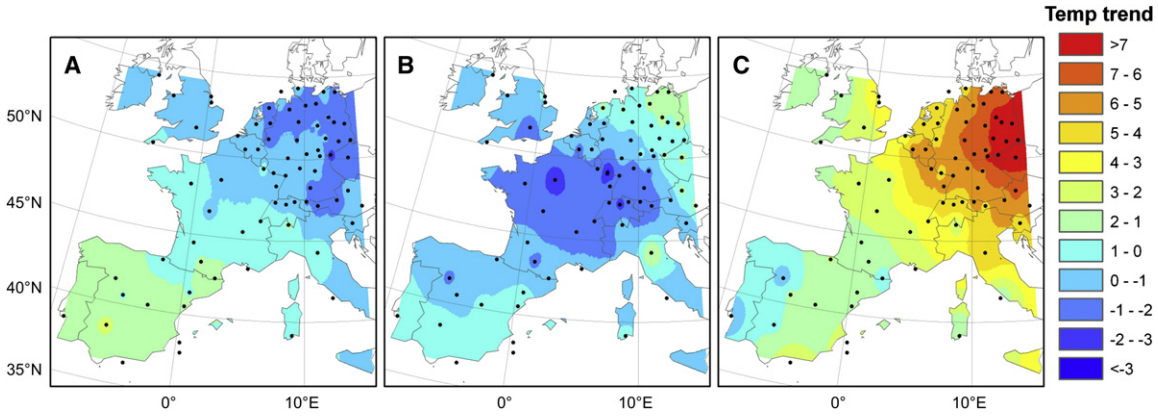

Figure 4. Spatial Variation in Temperature Trends from 1980 to 2001 during Migration for Pied Flycatchers Migrating from Northern Africa to Breeding Sites at 52°N

(A) Temperature trend (as slope of linear regression of annual mean on year for the period 1980–2001) for the period 8 days before the date of median passage.

(B) Temperature trend at the date of median passage.

(C) Temperature trend 8 days after the date of median passage. Data are from [35]. For each site, average temperatures during the 10-day period before the focal date were taken. Note that the focal date differs by 6 days between Southern Europe and the 52°N breeding site.

be solved by simple phenotypic or evolutionary responses toward earlier phenology. An adaptive evolutionary response most likely is needed on a whole suite of different traits simultaneously, and it remains to be seen whether evolution can alter species quickly enough to stop their decline.

Experimental Procedures

This study was performed on the pied flycatcher (*Ficedula hypoleuca*), a long-distance migrant passerine that breeds in large parts of Europe and Western Asia and winters in Western Africa around 10°N [13]. The species breeds readily in nest boxes, and therefore large numbers of young are ringed each year in several European countries. The breeding ecology of the species is well known [11, 14], and it is one of the long-distance migrants for which we have the most detailed knowledge about its response to climate change [5, 6, 29].

Data Selection and Analysis of Recoveries

Data on recoveries of pied flycatchers were provided by the national ringing centers of Denmark, Finland, Germany, The Netherlands, Norway, Sweden, and the United Kingdom via the EURING network. I selected individuals that were ringed as nestlings and were recovered between 30°N and 38°N in the period from March 1 through June 3 and only excluded cases for which too little information was available to assign a recovery date. In these countries, over 2.2 million pied flycatcher nestlings have been ringed during the last 35 years, which makes this bird probably the long-distance migrant most commonly ringed as a nestling. I selected the cases in which the date of recovery was considered to be within 2 days of the death of the bird, but the date of recovery may not be exact in some cases, because this depends on the accuracy of judgment of the finder. I used recoveries over a large latitudinal range in Northern Africa and southern Spain (Figure 1; collectively referred to as Northern Africa because most of the recoveries were made there) and included finding latitude and longitude in the analysis of recovery date. If finding latitude and/or longitude were significant (one analysis), they were retained in the final model, but for the significance of the other variables, it did not matter whether these were retained or not.

The recoveries spanned the period between March 1 and June 3, with a peak around April 20. Recoveries were made between 1949 and 2002, with most between 1972 and 1993 (see the Supplemental Information available online). Recovery dates were analyzed in two ways: as medians on a larger spatial scale ("population level") and as individual recoveries. For the population level, I calculated the median recovery date of birds born in blocks of 3° latitude × 3° longitude in order to produce a reasonable estimate for local breeding populations. Only if there were more than nine recoveries did I use the data for that particular block; in other cases, I took the data from two to six consecutive blocks together to have at least nine recoveries. I analyzed the effect of birth latitude by regressing the median recovery date for each block against the mean latitude and longitude of birth for that particular block. Ringing latitude was always used as a continuous variable in the models, but for explaining how the effect of birth date varies with latitude, I give estimates for certain locations. In the graphs, I have divided the data into arbitrary latitude categories for presentation purposes only, to visualize the differential effect of latitude. The effect of latitude and longitude on timing of migration was compared with the effect of latitude and longitude on the timing of breeding; for this, data from Sanz [14] were used, supplemented with data from Russia [11]. Only data from latitudes higher than 48°N were used, because I had no recovery data from more southern populations. I also collected data on arrival dates for different breeding populations; for this, I used data for which a large fraction of the population of both males and females had been sampled. The median arrival date was calculated for each year for both sexes separately, the different years were averaged per sex, and the mean of the two sexes was then taken. Data were from previous publications [30–32], supplemented with unpublished data from Oulu, Finland (provided by Forsman and Seppanen [33]) and southern Finland (provided by T. Laaksonen, personal communication) and my own data collected in The Netherlands.

For the analysis of whether spring recovery date in Northern Africa was related to birth date, I approximated birth date with ringing date of nestlings. Pied flycatcher nestlings can be safely ringed from 7 days of age, until about 13 days, when they fledge. The inaccuracy in estimation of birth date will add variation to the data and hence will make tests conservative. Within populations, the variation in birth date is about 20 days, which is considerably greater than the inaccuracy in the estimates. In a mixed model with normal errors, I used recovery date as the dependent variable; finding latitude and longitude, ringing latitude and longitude, ringing date, recovery age (with two levels: recovered in the first spring, or recovered in later springs), and the two-way interactions between these dependent variables as independent variables; and year as a random effect. Only the significant interactions are shown. I used a backward elimination procedure, and significance levels are given with only the significant variables in the model. All p values were two sided. Effect sizes are given with their standard errors in parentheses.

Data on Timing of Breeding

For the analysis of whether birds breed earlier when they are born earlier in the year and of whether early-born offspring thus have early-migrating offspring, I used data on laying and hatching dates of a ringed population breeding in nest boxes in The Netherlands (Hoge Veluwe National Park; 52°02′ N, 05°51′ E) between 1960 and 2005. Nests are checked weekly, and laying dates are back calculated assuming that one egg is laid every day (laying date is day of first egg). Visits to the nests are more frequent before hatching, and hatching date is defined as the day that the first egg hatched. All chicks are ringed, and parents are caught and identified on

the basis of their rings when feeding the brood (see [34] for more details). The analysis performed in this paper is of whether birth date of young correlates with the laying date of recruiting females. For this, I used the laying date for each female when she was first caught as a breeder in the area and included age with two levels: one-year-old females versus older females. Not all females are caught in their first year, because they escape being caught, do not breed, or breed outside the study area. I used residuals to the mean of the year to account for annual differences and the clear change in laying date over the period 1980–2005 [34].

Analysis of Temperature Trends during Migration

As environmental conditions encountered en route at different migration times, I considered temperatures, because these determine both insect availability (for insectivores) and energy expenditure of the birds. I aimed to describe the means and trends in temperatures that the birds would encounter during their actual migration at different sites from Northern Africa to Europe. For this, I took the median date on which the birds passed through Northern Africa and the median date on which the birds arrived at their breeding grounds and assumed that birds migrated with constant speed between these sites. For each site along the migratory route, I calculated the mean temperatures over the 10-day period before calculated median passage. This environmental measure gives the actual circumstances during average passage and is also a proxy for the recent phenological development. I investigated the spatiotemporal variation in temperature changes that the birds would encounter when migrating at different times by calculating the temperature trends for the period 8 days before the median passage date (Figure 4A), at the median passage date (Figure 4B), and 8 days after the median passage date (Figure 4C). I calculated trends in temperature between 1980 and 2001 for each migration period by calculating the slope of the linear regression of mean temperature for each 10-day period and year. This analysis was only performed for birds breeding at 52°N, because these populations have advanced their laying date as well as their migration date through Northern Africa, but not their arrival at the breeding grounds.

Daily temperature data were taken from 75 weather stations across Europe obtained from http://eca.knmi.nl/dailydata/index.php [35]. I selected those stations that had daily temperature data from 1980 through at least 2000 and at most 2001. If two stations were less than 1° apart in distance, I selected only one, because temperature data are strongly spatially correlated. Isocline maps of temperature trends were calculated based on 12 weather stations by using universal kriging with a circular semivariogram model in ArcGIS software version 9.2. This interpolation method gives weight to the distance of a point to the measured points based on spatial correlation, rather than giving weight based only on the distance to the measured points (inverse distance interpolation).

Supplemental Information

Supplemental Information includes one figure and can be found with this article online at doi:10.1016/j.cub.2009.11.074.

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